Draft Report to Placer County

Butterfly Community Change in Response to Rural Residential Development

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ABSTRACT

This study examined changes in butterfly community structure in response to rural residential development in the oak-woodlands of central California. Rural residential development is associated with the replacement of native habitat with new habitat types and alteration of hydrologic and disturbance regimes. Small parcel size was positively correlated with the diversity of habitat and negatively related to the percent area of native habitat at sites across the range of parcel sizes observed; this suggests that parcel size may be a useful management tool for influencing native habitat conservation. Species richness at sites was negatively related to parcel size, positively related to habitat diversity, and peaked at intermediate levels of percentage native habitat area at a site. However, the loss of native habitat associated with smaller parcel sizes resulted in the loss of native habitat-limited species. The ability of a species to exploit or persist in human-altered environments depends on its life history characteristics. While vagility did not influence the distribution of butterfly species, the numbers of hostplant specialists and univoltine species were positively correlated with the percent area of native habitat at a site. Further, the numbers of multivoltine species and hostplant generalists were higher at sites with smaller parcels and higher percent area of modified habitat. These trends represent a shift in butterfly species composition from specialist to generalist species with increasing urbanization. This study provides evidence for the importance of parcel size in butterfly conservation, but maintaining native habitat, even on small parcels, helps retain native habitat-limited butterfly species.

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INTRODUCTION

Habitat loss and fragmentation affect biodiversity by causing both expansions and constrictions of species' ranges, resulting in changes in species composition and overall diversity (McKinney and Lockwood 1999). Most conservation efforts have long been concentrated on public lands and nature reserves. This trend, however, overlooks the extreme importance of biodiversity conservation on private lands, particularly for ecosystems in which most of the land is privately owned. For conservation on private lands to be successful it is critical to understand how biodiversity is affected by habitat changes resulting from different intensities of urban development.

The oak-woodlands of central California represent an ecosystem under considerable threat from increasing fragmentation and habitat modification due to urbanization. The western foothills of the Sierra Nevada are characterized by hardwood forest dominated habitats comprised of fairly continuous oak-woodland, grassland, and chaparral that extend approximately 400 miles from Lassen to Kern counties (1500-4000 ft) in California. Human population in this region is rising rapidly, and Placer County's is the fastest growing in California with a growth rate of 3.5 percent in 2000 (California Department of Finance 2001). This growth is resulting in increased residential development and associated habitat degradation. Thus far, habitat loss and degradation in the region has not resulted in the listing of species as threatened or endangered under the Endangered Species Act of 1973, but with increasing pressure for reductions in parcel size and continual development, anticipatory planning at this juncture may be important to prevent future listings. More than eighty percent of blue oak-woodlands in California (Davis et al. 1998), and 93 percent of such woodlands in Placer County, California, are in private ownership (Placer County Planning Department 2000). Thus, private lands are critical for maintaining oak-woodland biodiversity.

County planning departments tend to have limited regulatory control over private land use. However, they do control parcel size zoning, which may prove to be a useful tool for implementing private land conservation efforts. This study examines the effects of zoning on habitat and butterfly diversity.

Butterflies were selected as the focal taxon for this study for several reasons. Butterflies have been shown to respond both to changes in vegetation and alteration of disturbance and hydrologic regimes that result from rural residential development. Butterflies have been suggested as indicators of ecological change because they are closely dependent on specific species of plants during several stages of their life cycles, and they are sensitive to environmental changes including local weather, climate, and light levels that are affected by habitat disturbance (Watt et al. 1968, Ehrlich et al. 1972, Weiss et al. 1987, 1988, Hill et al. 1995, Blair and Launer 1997, Wood and Gilman 1998, Kitahara and Sei 2001).

Further, the butterfly fauna associated with the Sierra Nevada foothills is well documented and has been characterized to some extent with respect to habitat associations. Some butterfly species are specialists limited in distribution by specific habitat such as oak-woodland, while others are weedy generalists that can use a wide variety of often highly modified habitats including widespread or weedy plant species that have characterized the central valley since its conversion to agriculture (Shapiro). This diversity in host plant and habitat specificity among butterfly species provides an unique perspective in which to view the changes in butterfly community composition associated with rural residential development. A shift towards increased numbers of generalist species and decreased numbers of specialist species in human modified environments has been documented for a variety of taxa including butterflies in several ecological systems (Kitahara and Fujii 1994, Kitahara et al. 2000, Kitahara and Sei 2001).

Understanding the consequences of parcel size reduction and its attendant modification and fragmentation of habitats can be important to developing policy and educational programs that will minimize the loss of biodiversity. This study examines the relationship between parcel size and habitat characteristics, determines how these habitat characteristics influence butterfly community composition, and identifies patterns of community change with respect to specialist and generalist species.

METHODS

Study Area and Site Selection:

Study sites were located in the western foothills of the Sierra Nevada in Placer County, California, along the route 49 corridor extending north of Auburn, California. This area was historically dominated by blue oak-woodland. Currently this area is a mosaic of second growth oak-woodland, pastureland, and habitat associated with rural residential development such as lawns, gardens, and cultivated shrubs. The intensity of development in this study ranges from sites with 0.4 hectare (one acre) parcels and highly modified vegetation to greater than 81 hectare (200 acre) parcels characterized by undeveloped oak-woodland.

Twenty-six study sites were chosen based on parcel size and elevation using a G.I.S. database of Placer County parcel information. Areas of similarly sized, contiguous parcels were identified, and study sites were established within these regions. Sites were selected to have a surrounding buffer of land with levels of urbanization similar to that of the site to minimize edge effects. Sites were chosen systematically with respect to parcel size to encompass the full gradient of urbanization, but sites were selected at random with respect to other characteristics including land-use and area of remaining oak-woodland. All sites were between 250 and 450 meters in elevation and were located within an area 20 kilometers north to south and 6 kilometers east to west in Placer County, California. Permission to access each site was obtained from land-owners.

Butterfly Sampling:

Each site was sampled for day-flying Papilionoidae and Hesperiidae, henceforth referred to as butterflies, a total of nine times between May 25 and August 20, 2000, and between April 16 and May 18, 2001. Sites were sampled about once every two weeks for one to 1.5 hours each using the visual encounter survey technique described by Crump and Scott (1994). Although sampling time varied across sampling periods, all sites were surveyed for the same amount of time within a given sampling round. Sampling was limited to days when weather was conducive

to butterfly flight. For each visit to a site, all species observed were recorded; species that were difficult to identify in the field were collected for later identification.

Sites were sampled so that at least one site representing high density development (0.4 to 1.2 hectare (one to three acre) parcels), medium density development (1.8 to 8.1 ha (4.5 to twenty acre) parcels), and low density development (greater than 8.1 ha (twenty acre) parcels) were sampled each day to minimize effects of daily variation. In addition, each site was sampled alternately in the afternoon and morning in consecutive visits.

Landscape Variables:

Because butterflies could disperse into a site from adjacent areas, site characteristics were analyzed for an area that included both the sampling site and a 100 meter buffer surrounding it.

Color aerial photographs were used to identify habitat types within study sites and were digitized and attributed using G.I.S. (ESRI ArcView GIS 3.2). Field surveys were used to corroborate habitat type identification. Habitat was classified into five habitat categories. 'Native habitat' included all uncultivated areas characterized by oak-woodland. 'Mowed oak-woodland' was oak-woodland with an uncultivated, but periodically mowed, understory. 'Grassland' was uncultivated grassland, characterized primarily by annual grasses. 'Cultivated areas' included all irrigated land, ornamental vegetation, mowed grasslands, and other non-native or cultivated vegetation. The final habitat category was 'non-habitat' and included all non-vegetated areas, including buildings, roads, and pavement. All variables were measured as the percent of land in that habitat type at a site.

Parcel size was measured as the weighted average of the log transformation of parcel size for all parcels within each site and buffer. Habitat diversity was calculated using the Shannon-Weaver diversity index (Magurran 1998). This index was calculated using proportion of total habitat, excluding 'non-habitat', that was represented by each habitat type.

Data analysis:

We calculated species richness as the total number of species observed at a site across all sampling periods. Species occurrences were defined as the number of visits to a site during which the species was observed (i.e. species occurrences could range from 0 to 9, the total number of visits to each site). Migratory species, including *Nymphalis* spp., *Danaus plexippus*, and *Vanessa* spp., were excluded from the analyses in this study. In addition, *Erynnis tristis* and *E. funeralis* and *Satyrium californica* and *S. sylvinus* were not differentiated in the field. Thus *Erynnis* sp. and *Satyrium* sp. were included in analyses of total species richness but were omitted from all other analyses. Species that occurred at only a single site (i.e. *Lycaena helloides*, *Celastrina ladon*, *Glaucopsyche lygdamus*, *Pieris napi*, and *Pontia protodice*) were also excluded from all analyses except total species richness.

Site characteristics:

Site characteristics, including habitat diversity and percent area of non-habitat, cultivated area, mowed oak-woodland, native habitat, and grassland, were fit as linear functions of the natural log of parcel size (Table 1). Percent areas of each habitat type were converted to proportions and transformed using an arcsine square-root transformation prior to fitting each model.

In addition, habitat diversity was modeled as a quadratic function of the percent area of native habitat at each site.

Species richness:

Species richness was fit as five separate functions of site characteristics to compare the explanatory value of each variable (Table 2). Site characteristics included in these models were habitat diversity, the natural log of parcel size, and the percent area of native habitat at each site.

Influence of Site Characteristics on Species' Distributions:

Canonical Correspondence Analysis (CCA) was used to determine the influence of the habitat variables and parcel size on the distribution and occurrences of individual butterfly species. Analyses were conducted using the program PC-ORD (Version 4, MJM Software). A Monte Carlo test with 499 iterations was used to test the null hypothesis that no relationship exists between the environmental variables and species distributions.

CCA is a constrained ordination gradient analysis technique that incorporates unimodal responses of species to environmental variables. This technique performs well with skewed species distributions and intercorrelated variables (Palmer 1993). CCA maximally separates species and sites along axes, but, unlike indirect gradient analyses, the axes are constrained to be linear combinations of the environmental variables. The eigenvalues produced by CCA measure the separation of species along ordination axes (Ter Braak 1987).

Classification of species as oak-woodland specific and disturbance tolerant:

To classify species as native habitat-limited or disturbance tolerant, a logit model was constructed for each butterfly species to examine its probability of occurrence with respect to the percent area of native habitat at a site (Table 3). Species were categorized as native habitat-limited if the coefficient on 'native habitat' was positive and the probability of the slope coefficient equaling zero was less than five percent, according to the G statistic calculated from the log-likelihood value. Similarly, species were classified as disturbance tolerant if the coefficient on 'native habitat' was negative and the slope coefficient was significant at the five percent probability level.

We modeled the percentage of native habitat-limited species present at a site as separate linear functions of the percent area of native habitat and the natural log of parcel size (Table 4). To determine the suitability of mowed oak-woodland and grassland for supporting these habitat-

specific species, we alternately added these habitat variables to the model that included percent area of native habitat (Table 4).

Species' life history characteristics and responses to habitat change:

Logistic regression was used to assess the influence of species' life history characteristics on the probability of species occurring at sites that differed in their percent area of native habitat. Specifically, the importance of interactions between percent area of native habitat and species' larval hostplant breadth, vagility, and voltinism in predicting species occurrences, was examined. This analysis was conducted using the program Mini-tab (Release 12, Microsoft Corp). Variables included in this analysis were percent area of native habitat, hostplant breadth, voltinism, vagility, and interactions between percent area of native habitat and hostplant breadth, voltinism, and vagility, respectively (Table 5). Interaction terms were calculated by centering both variables (subtracting the mean) and taking their product.

Hostplant specificity and voltinism data for each butterfly species were taken from Garth and Tilden (1986). Species hostplant specificity scores ranged from 1 to 4 depending on the taxonomic breadth of their larval feeding (Appendix 1). Species which feed only on one plant species were scored as 1; butterflies that feed on plants from only one genus were scored as 2; butterflies that feed on species limited to one family were scored as 3; and butterflies that feed on species from more than one family were scored as 4. Voltinism scores equaled the typical number of broods for the species (Appendix 1). If a range was provided for the number of broods, the average of that range was used for the score. Likewise, "multiple" and "many" broods were scored as three broods.

Vagility estimates were provided by George Austin (pers. communication.) and scored as in Fleishman et al. (1997) (Appendix 1). Species that disperse tens of meters were scored as 1, hundreds of meters were scored as 2, thousands of meters were scored as 3, and ten thousands of meters and higher were scored as 4.

A second set of analyses was conducted to determine whether the patterns of voltinism and hostplant breadth across the habitat gradient identified by the logit model were the result of species additions, deletions, or both. Species were categorized as specialists and generalists with respect to both voltinism and hostplant breadth. Species were categorized as seasonal generalists if they have greater than two broods per year and as seasonal specialists if they are univoltine. Likewise, species were categorized as feeding specialists if they feed on species from a single genus and as feeding generalists if they feed on species across several plant families.

The richnesses of seasonal specialists and univoltine species were modeled as quadratic functions of the percent area of native habitat at sites to allow for a non-linear response to habitat change (Table 6). Models were reduced if the quadratic term was found to be non-significant ($p>0.05$). The richnesses of feeding and seasonal generalists were modeled as functions of the percent of native habitat area at sites, habitat diversity, and the natural log of parcel size to examine the explanatory value of these aspects of urbanization (Table 6).

Seasonality:

To understand how species with different seasonal characteristics utilized habitat between seasons, we modeled species richness and richnesses of univoltine and multivoltine species as functions of percent area of native habitat, season, and habitat/season interactions (Table 7). Site visits were categorized as spring or summer and richnesses were calculated for each site and season. Spring included all visits during which at least some understory in native habitat remained green (unsenesced). These included the first two visits in 2000 (May 25 to June 18) and the three visits in spring 2001 (April 16 to May 18). Summer included those visits during which the understory of the native habitat was completely dried, which were the last four visits in 2000 (June 21 to August 20).

RESULTS

Site Characteristics:

The 26 sites in this study ranged in average parcel size from approximately 0.4 to 81 hectares (one to 200 acres). A linear function of the natural log of parcel size explained 57.2, 78.1, 46.8, 55.2, and 36.5 percent of the variation in habitat diversity and percent area of non-habitat, cultivated habitat, mowed oak-woodland, and native habitat, respectively (all habitat characteristics were arcsine square root transformed) (Figure 1 a-e; Table 1). There was no linear relationship between parcel size and percent area of grassland (Figure 1 f; Table 1).

Habitat diversity was related to percent area of native habitat as a quadratic function (F-test; d.f. = 2, 23; $p < 0.001$; $r^2 = 91.3$ %; Figure 2).

Species Richness:

Including migrants and rare species, fifty species of butterflies were observed during nine visits to each of 26 sites. Species richness reached a maximum at intermediate levels of remaining native habitat and was significantly related to the percent area of native habitat at a site as a quadratic function (F-test; d.f. = 2,23; $p = 0.014$; $r^2 = 31.1$ %; Figure 3a; Table 2). Species richness was negatively, linearly correlated with the natural log of parcel size (F-test; d.f.= 1,24; $p = 0.005$; $r^2 = 28.5$ %; Figure 3b; Table 2) and positively linearly related to habitat diversity (F-test; d.f.= 1,24; $p = 0.020$; $r^2 = 20.4$ %; Figure 3c; Table 2). No additional variance in species richness was explained by including habitat diversity into the models that included native habitat or parcel size (Table 2). However, a function including a linear response to the natural log of parcel size and a quadratic function of the percent area of native habitat explained 43.8 % of the variance in species richness (F-test; d.f. 3,22; $p = 0.005$; Table 2) with correlation between characteristics maintaining the same sign.

Influence of Site Characteristics on Species' Distributions:

The Canonical Correspondence Analysis showed that landscape-level habitat characteristics did influence the distribution of butterfly species (p<0.01) and that percent areas of native habitat and cultivated habitat were the land cover variables most important in determining the distribution of species (Figure 4). The first ordination axis was significant (p=0.002) and explained 23.8 percent of the total variance in species. This axis was most correlated with the percent area of native habitat at sites (intra-set corr: 0.971; inter-set corr: 0.926). The percent area of cultivated habitat was also highly, but negatively, correlated with the first ordination axis (intra-set corr: -0.834; inter-set corr: -0.795). A significant relationship existed along the first ordination axis between the environmental variables and species distributions and occurrences (p=0.002). The second and third ordination axes were not significant (p>0.05) and explained little additional variance in the data (5.4 and 3.7 percent, respectively). The relationship between species distributions and area of native habitat is further illustrated in Figure 5.

Classification of species as oak-woodland specific and disturbance tolerant:

Nine species were identified as limited to native habitat based on the results of the logistic regressions (Table 3). These were *Anthocaris sara, Zerene eurydice, Adelpha bredowii, Cercyonis sthenele, Euphydryas chalcedona, Erynnis propertius, Hesperia colorado, Ochlodes agricola,* and *Satyrium auretoreum*. Ten species were identified as being limited to modified habitat (Table 3). These species were *Pieris rapae, Polites sabuleti, Pyrgus communis, Pholisora catullus, Hylephila phyleus, Junonia coenia, Phyciodes mylitta, Everes comyntas, Limentis lorquini,* and *Strymon melinus*. All other species showed no significant response to the percent area of native habitat at sites (p > 0.05; Table 3).

The percent of native habitat-limited species occurring at a site declined linearly with decreasing percent area of native habitat (F-test; d.f. = 1,24; p<0.001; r^2=66.7%; Figure 6a; Table 4) and with decreasing parcel size (natural log transformed) (F-test; d.f. = 1,24; p=0.007;

r^2=26.3%; Figure 6b; Table 4). A linear model including percent areas of both native habitat and grassland explained 69.2 % of the variance in richness of native habitat-limited species, but the coefficient on grassland was not significant (*t*-test; p=0.184; Table 4). Likewise, area of mowed oak-woodland did not significantly explain additional variance (*t*-test; p=0.959; Table 4).

Species' life history characteristics and responses to habitat change:

The interactions of hostplant breadth with percent area of native habitat and of voltinism with percent area of native habitat were both significant in the logit model of species occurrences (ind. t-tests; d.f. = 537; p<0.001; Table 5). Species that feed on a narrow breadth of larval hostplants or that have low voltinism had a higher probability of occurrence at sites with more native habitat than at sites where native habitat had been replaced by alternative habitat types, relative to species with wide hostplant breadth or high voltinism. Vagility was unrelated to species distributions across sites (p>0.05; Table 5).

The number of univoltine species declined linearly with loss of native habitat (F-test; d.f. = 1,24; p<0.001; r^2=54.1%; Figure 7 b; Table 6). The number of hostplant specialists also declined with loss of native habitat, but peaked at intermediate areas of remaining native habitat (F-test; d.f.=2,23; p<0.001; r^2=49.3%; Figure 7 a; Table 6). The richness of multivoltine species was best explained by a quadratic function of percent area of native habitat and a linear response to the natural log of parcel size (F-test; d.f.=3,22; p<0.001; r^2= 87.7%; Table 6). However, richness of multivoltine species also was explained well by a simple quadratic function native habitat area (F-test; d.f.=2,23; p<0.001; r^2= 82.5%; Figure 7 d; Table 6) in which richness increased with declining native habitat area but peaked at intermediate levels and by a positive linear function of habitat diversity (F-test; d.f.=1,24; p<0.001; r^2= 82.8%; Figure 7 f; Table 6). The most variance in richness of feeding generalists was explained by the quadratic function of percent area of native habitat with a linear parcel size term (F-test; d.f.=3,22; p<0.001; r^2= 74.6%; Table 6), but the coefficient on the quadratic term of native habitat was not significant (t-test; d.f.

$= 22$; $p = 0.131$). The richness of feeding generalists was also well explained by a positive linear function of habitat diversity (F-test; d.f.=1,24; $p<0.001$; $r^2= 70.8\%$; Figure 7 e; Table 6) and by a quadratic function of percent area of native habitat (F-test; d.f.=2,23; $p<0.001$; $r^2= 61.9\%$; Figure 7 g; Table 6) that modeled its increase and plateau with loss of native habitat.

Seasonality:

Species richness peaked at intermediate levels of native habitat during spring but declined with increasing percent area of native habitat during summer (F-test; d.f. = 4,47; $p<0.001$; $r^2= 61.8\%$; Table 7; Figure 8 a). Richness of univoltine species was higher during spring than during summer and was higher at sites with a greater percent of native habitat area during both seasons (F-test; d.f. = 3,48; $p<0.001$; $r^2= 54.1\%$; Table 7; Figure 8 b). Richness of multivoltine species was highest at intermediate levels of native habitat in spring but declined with increasing percent area of native habitat in summer (F-test; d.f. = 4,47; $p<0.001$; $r^2= 68.4\%$; Table 7; Figure 8 c).

DISCUSSION

Many studies have addressed the responses of butterflies to various types of habitat

disturbance (Kremen 1992, Kitahara and Fujii 1994, Hamer et al. 1997, Kitahara et al. 2000,

Kitahara and Sei 2001), including some that have addressed butterfly response to habitat changes

associated with urbanization (Shapiro and Shapiro 1973, Yamamoto 1977 (cited in Ruszczyk

1986), Ruszczyk 1986, Ruszczyk and De Araujo1992, Blair and Launer 1997, Merenlender et al.

1998). However, of the studies addressing disturbance associated with urbanization, only one

(Merenlender et al.1998) did not focus on changes in highly urbanized areas. Although studies of

highly urbanized areas are important for understanding the suitability of those areas to support

biodiversity, they provided little information regarding changes associated with low intensity

development that impacts a much more extensive area of the landscape.

Blair and Launer (1997) identified an overall decline in butterfly richness with urbanization

of oak-woodlands, with maximum species richness at intermediate levels. Blair and Launer

(1997) also showed that species characteristic of the pristine oak-woodland condition dropped out

at sites with increased urbanization. The applicability of these results are limited, however, by the

lack of replicates, limited number of sites (six), and the lack of a metric for measuring

urbanization.

Merenlender et al. (1998) examined butterfly diversity change in the oak-woodlands of

California across a gradient of rural residential development. Sites were selected with the

criterion of having some amount of hardwood cover, and all sampling was conducted within

those areas. Thus, results of the study only addressed diversity changes within oak-woodland

habitat and could not be linked to parcel size independent from site characteristics.

Our study was based on measurable aspects of urbanization, including parcel size and percent

area of remaining native habitat, that can be applied to other situations. We looked at study sites

characterized by parcels ranging in size from approximately 0.4 to 81 hectares (one to 200 acres),

a gradient along which all sites maintained some area of native habitat. However, we sampled across all habitat types to assess total butterfly community change associated with rural residential development.

Patterns of community change:

Habitat change:

Urbanization affects plant communities both directly and indirectly. Because much of the influence of rural residential development on faunal communities likely results from changes in vegetation, it is important to understand the relationship between parcel size and habitat characteristics. Percent area of non-habitat, cultivated habitat, and mowed oak-woodland at sites were all negatively correlated with the natural log of parcel size (Table 1) and tended asymptotically to zero with increasing parcel size so that the area of these habitat types was negligible at parcel sizes 10 hectares and larger (Figure 1 b, c, d). Likewise, the percent area of native habitat tended to increase linearly with the natural log of parcel size (Table 1), and variance was lowest at parcel sizes greater than 10 hectares (Figure 1 e). The percent area of grassland appeared to be low on small and large parcels and was extremely variable across mid-sized parcels, but was not linearly related to the natural log of parcel size (Figure 1 f; Table 1).

Habitat diversity tended to increase with decreasing parcel size (Figure 1 a; Table 1) but peaked at intermediate levels of percent area of native habitat (Figure 2). The intermediate disturbance hypothesis suggests that richness or diversity will peak at intermediate levels of disturbance because of the influence of disturbance on the competitive balance among species (Connell 1978). Although forces other than competition are likely responsible for determining the relationship between habitat diversity and rural residential development, the peak in habitat diversity at intermediate levels of native habitat lends support to the functioning of urbanization as a form of disturbance, measured, in this case, by loss of native habitat.

Species richness:

We found that species richness was positively correlated with housing density (Figure 3 b; Table 2) and peaked at intermediate levels of percent area of remaining native habitat (Figure 3 a; Table 2); parcel size and percent area of native habitat together explained 43.8 % of the variance in species richness. Because habitat diversity also peaked at intermediate levels of native habitat (Figure 2) and was linearly related to the natural log of parcel size (Figure 1 a; Table 1), the relationship between species richness and native habitat area and parcel size may reflect a relationship between species richness and habitat diversity. Natahura et al. (1999) suggested that habitat mosaics can increase species richness through both the creation of edge habitat and the increase in habitat diversity. However, our study showed that, although habitat diversity was significantly related to species richness, it explained less of the variance (20.4%) than did parcel size (28.5%) or percent area of native habitat (31.1%) (Table 2).

Because habitat diversity does not adequately explain the relationship between species richness and parcel size or native habitat area, some other characteristic of residential density may additionally increase species richness. Irrigation, specific habitat types, or increased nectar availability associated with higher residential densities may be responsible for this additional increase in species richness. Likewise, butterfly species richness fits the pattern predicted by the intermediate disturbance hypothesis (Connell 1978) with disturbance measured as the loss of native habitat.

Seasonality is an aspect of species richness that is often ignored but may have important ramifications for data interpretation. In this study species richness peaked at intermediate levels of native habitat during spring but declined with increasing area of native habitat during summer (Figure 8a; Table 7). Thus, conclusions regarding the diversity of butterflies with respect to habitat would have been very different had we sampled only in spring or in summer. Some studies of butterflies and disturbance have failed to sample across the temporal range of their

focal community (Hill et al. 1995, Hamer et al. 1997, Spitzer et al. 1997, Wood and Gilman 1998). This omission could affect studies looking at butterfly community changes across environmental gradients since season is likely to influence habitat types and disturbance levels differently.

Species-specific responses to decline of native habitat:

The percent area of native habitat was the most important characteristic for determining species composition (Figure 4). The species that were highly responsive to oak-woodland decline were *Anthocaris sara, Zerene eurydice, Adelpha bredowii, Cercyonis sthenele, Euphydryas chalcedona, Erynnis propertius, Hesperia colorado, Ochlodes agricola,* and *Satyrium auretoreum* (Table 3, 8). Of these species, five were included in the study by Blair and Launer (1997). *Hesperia colorado[comma], Ochlodes agricola, Erynnis propertius,* and *Euphydryas chalcedona* were classified as urban avoiders, but *Anthocaris sara* was classified as suburban-adaptable in their study (Table 8). Because they found *Anthocaris sara* only at three visits to a single site, its absence from the least urbanized site likely results from the infrequency of observation rather than a true preference for the more urbanized site. Merenlender et al. (1998) also found *Euphydryas chalcedona, Erynnis propertius,* and *Ochlodes agricola* in their study, but they did not detect any significant differences in the distribution of these oak-woodland preferring species across their gradient (Table 8).

In this study *Pieris rapae, Polites sabuleti, Pyrgus communis, Pholisora catullus, Hylephila phyleus, Junonia coenia, Phyciodes mylitta, Everes comyntas, Limentis lorquini,* and *Strymon melinus* were largely absent from sites characterized by native habitat (Table 3, 8). However, *Pieris rapae, Pyrgus communis, Junonia coenia,* and *Phyciodes mylitta* were also observed in the Merenlender et al. (1998) study in which all sampling was done in oak-woodland habitat (Table 8). It is surprising that Merenlender et al. (1998) observed no trends in the distribution of these species, unless their observations were primarily of strays and small sample sizes prevented the

detection of a trend. However, Shapiro (1980, 1987) supported our classification of the above species, except for *Limentis lorquini* which he did not sample, and referred to them as "weedy," widespread species in the Central Valley, California (Table 8). Blair and Launer (1997) also supported our classification, except for *Pholisora catullus*, *Everes comyntas*, and *Limentis lorquini* which they did not observe (Table 8). Blair and Launer also identified several other species as suburban-adaptable and urban-avoiders that showed no significant response to the area of native habitat in our study. This may be a construct of the shorter urbanization gradient examined in this study.

Life History Characteristics:

In this study we tested the hypotheses that species showing univoltinism, high hostplant specificity, and low vagility are associated with more native sites, whereas species characterized by multivoltinism, wide hostplant breadth, and high vagility are associated with more urbanized sites. We found no relationship with vagility but did find relationships between species distributions and hostplant specificity and voltinism (Table 5).

Vagility is expected to be important in determining the success of a species in a highly fragmented landscape. However, in this study, habitat patches may not have been effectively isolated because of the scale of the mosaic examined, the quality of the matrix between habitat patches for dispersal, and the species' generally high vagility. (Only *Callophrys augustinus* was thought to regularly disperse fewer than hundreds of meters (Austin, personal communication; Appendix 1).)

Richness of species that feed on a single genus of plants declined with decreasing percent area of native habitat but had a moderate peak at sites with intermediate levels of native habitat (Figure 7 a; Table 6). Other studies also have shown that species limited to the most natural sites tend to have narrow hostplant breadth (Shapiro and Shapiro 1973, Shapiro 1987, Blair and Launer 1997). Steffan-Dewenter and Tscharntke (2000) showed that in calcareous grasslands

monophagous and oligophagous butterfly species were more affected by habitat area than were polyphagous species. Species that feed on a single genus of plants may be more likely to lose their larval food source than species that feed on a wider variety of plants when habitat area declines.

The richness of species that feed on plants from multiple families increased with the replacement of native habitat by other habitat types and peaked at intermediate levels (Figure 7 c; Table 6). Species that feed on a wide variety of plants may be more likely to utilize species that characterize the new vegetation types, particularly if the diversity of these habitats is high. In fact, a linear function of habitat diversity explained more of the variation in the richness of feeding generalists (70.8%; Figure 7 e; Table 6) than did the quadratic function of native habitat area (61.9%). However, including the natural log of parcel size into the model with native habitat area also increased the amount of variance explained (74.6%; Table 6). This supports the possibility that some aspect of small parcels, such as nectar availability, irrigation, or specific habitat types, increases habitat suitability for generalist species, and thus total species richness.

A pattern of decreasing numbers of univoltine species with decreasing native habitat was also significant (Figure 7 b; Table 6). Voltinism is a trait that is often associated with the predictability of a system as well as the length of the potential "growing season" (Shapiro 1975, Kitahara and Fujii 1994, Kitahara et al. 2000). Because summers in the foothills of the Sierra Nevada tend to have very little precipitation and because the understory of the oak-woodlands are dominated by annuals, the "growing season" for this system tends to be very short for many plant species (Shapiro 1975, Blair and Launer 1997). Univoltine species may be well adapted to the short growing season or have evolved to match the phenology of their short-lived hostplants (Shapiro 1975). This pattern is supported by the seasonal and habitat patterns identified for univoltine species in this study, in which richness was highest in the spring and at more native sites and was near zero both at highly modified sites and during summer (Figure 8 b; Table 7).

Shapiro (1987) observed that low-elevation species with univoltine life cycles that are adapted to summer drought are absent from the highly modified central valley, further supporting that these univoltine species will continue to decline with increasing habitat modification in the Sierra Nevada foothills.

The richness of multivoltine species increased with the reduction of percent area of native habitat but peaked at intermediate levels (r^2= 82.5%; Figure 7 d; Table 6). These species may be limited in their ability to reproduce in oak-woodland habitat because resources are not available throughout the season. Irrigation associated with urbanization may effectively lengthen the growing season by providing green vegetation and nectar through the summer, and thus irrigated areas may support species that were otherwise seasonally limited (Shapiro 1975, Blair and Launer 1997). This seasonal limitation is supported by the greater difference in the richness of multivoltine species between native and highly modified sites in summer than in spring (Figure 8 c; Table 7). Also, the addition of parcel size to the model with native habitat area was significant and increased the amount of variance explained (87.7%; Table 6). The increase in richness of multivoltine species with smaller parcels may reflect the influence of irrigation and extended growing season. However, habitat diversity also explained the richness of multivoltine species well (82.8%; Figure 7 d; Table 6), so it is difficult to separate the influences of these factors.

Framing these community changes in the context of generalist/ specialist species (Kitahara and Fujii 1994, Kitahara et al. 2000, Kitahara and Sei 2001) and relating them to r- and K-selection (MacArthur and Wilson 1967), enables these shifts to be viewed in an evolutionary context. Species that are associated with ephemeral habitats are expected to have characteristics that allow them to discover habitat quickly, reproduce rapidly, use up resources before they disappear, and disperse to find new habitat. The overall effect is to increase r, the intrinsic rate of increase. Thus, species adapted to unpredictable habitats are r-selected and tend to be generalists. Specialist species, on the other hand, tend to be associated with stable, predictable environments.

Multivoltinism in butterflies is considered an *r*-selected trait because of its associated short generation time and high reproductive potential that allows species to recover quickly after population declines (Shapiro 1975). Thus, the trend of decreasing specialist and increasing generalist species with decreasing native habitat and an overall increase in generalist species with decreasing parcel size is in accordance with ecological theory.

This shift from specialist to generalist butterfly species has been observed in other systems in response to various types of disturbance (Kitahara and Fujii 1994, Kitihara et al. 2000, Kitihara and Sei 2001). Framing butterfly community change in the specialist/generalist framework also is useful for understanding trends in biodiversity associated with urbanization.

Conservation Implications:

Having identified patterns of species turnover and a shift from specialist to generalist species with declining area of native habitat and smaller parcel sizes, it is important to consider how land-use decisions affect these patterns. Finding the appropriate balance between development and conservation is impossible without data, because it is unrealistic to expect that decisions supporting biological conservation will be made in the absence of data to justify straying from the economic optimum. Thus, data concerning the relationship between diversity and land-use is needed to optimize the balance between maximizing biodiversity and economic benefit.

We have shown that parcel size is an important determinant of both percent area of native habitat and species composition. The number of native habitat-limited species declined linearly with decreasing parcel size (Figure 6 b; Table 4), and parcels of 34 hectares (84 acres) and smaller supported, on average, fewer than 50 % of the native habitat-limited species identified in this study. Because smaller parcels have lower conservation value with respect to butterfly diversity than larger parcels, subdivision of smaller parcels will impact diversity at the landscape level less than subdividing large parcels. Since no sites sustained the full complement of native

habitat-limited species, protection of many large parceled sites is necessary to capture the full diversity of these species.

However, parcel size only explains 26.3 % of the variance in the number native habitat-limited species, while percent area of remaining native habitat explains 66.7 %. Thus, the influence of parcel size on butterfly diversity is determined primarily by its influence on the area of native habitat maintained. Sites maintaining less than 25 % native habitat area supported none or only one native habitat-limited species species (Figure 6 a), and sites with 71 % remaining area of native vegetation support, on average, fewer than 50 % of the native habitat-limited species identified in this study. No sites supported the full complement of native habitat-limited species, suggesting that extensive oak-woodland must be preserved in order to capture the heterogeneity and microhabitat characteristics required for all the species. Also, the density of many of these native habitat-limited species was low, further suggesting that large areas may be needed to maintain their populations. Therefore, concentrating development and leaving large areas of undeveloped habitat is likely important to maintain butterfly diversity. Blair and Launer (1997) agree and suggest that "if planners aim to maintain predevelopment levels of biodiversity, then any development should be concentrated."

Although maintaining large oak-woodland parcels is necessary for the conservation of native habitat-limited species, it is also important to note that large numbers of contiguous small parcels that maintain some native habitat do support some native habitat-limited species and thus are of conservation value. Because we demonstrated that neither grassland nor oak-woodlands with a mowed or irrigated understory are suitable for supporting native habitat-limited species, tree ordinances alone are unlikely to be effective in maintaining native habitat. However, tree ordinances combined with large parcel sizes may be relatively effective because landowners are not likely to irrigate or mow large expanses of oak-woodland. On large parcels, fire-risk can be

minimized close to structures through mowing and irrigation without impacting the greater extent of the parcel.

Large parcels also may be important for minimizing the risk of invasive plant species (Merenlender et al. 1998) and for supporting other uncommon butterfly species not represented in our samples. As development increases to the extent that total area of oak-woodland decreases and/or becomes more fragmented, butterfly diversity may decline faster than predicted from these data.

Importance of landscape-level studies and conducting research on private property:

This study focused on landscape-level habitat characteristics rather than detailed plant surveys and used presence-absence data instead of relative abundance for species. Nevertheless, we were able to identify important trends and relate those trends to management needs. Although detailed plant and animal surveys may be important in some circumstances, this study shows that less intensive habitat characterization may be sufficient, and perhaps more applicable, in many situations.

Focusing our research on private property was necessary to understand how best to conserve biodiversity in the California oak-woodlands (McDonnell and Pickett 1990, Blair and Launer 1997). Conducting research on private property has its difficulties; seeking permission from land-owners to access their property is time-consuming, and accessibility certainly restricts the ease of conducting research. However, interacting with land-owners also can be rewarding and help forward the cause of conservation by raising their awareness of species and habitat. During this study land-owners often expressed excitement in noticing butterflies they had never seen before and inquired about the number of species we had observed during this study. An awareness of the diversity of life is the first step towards its conservation.

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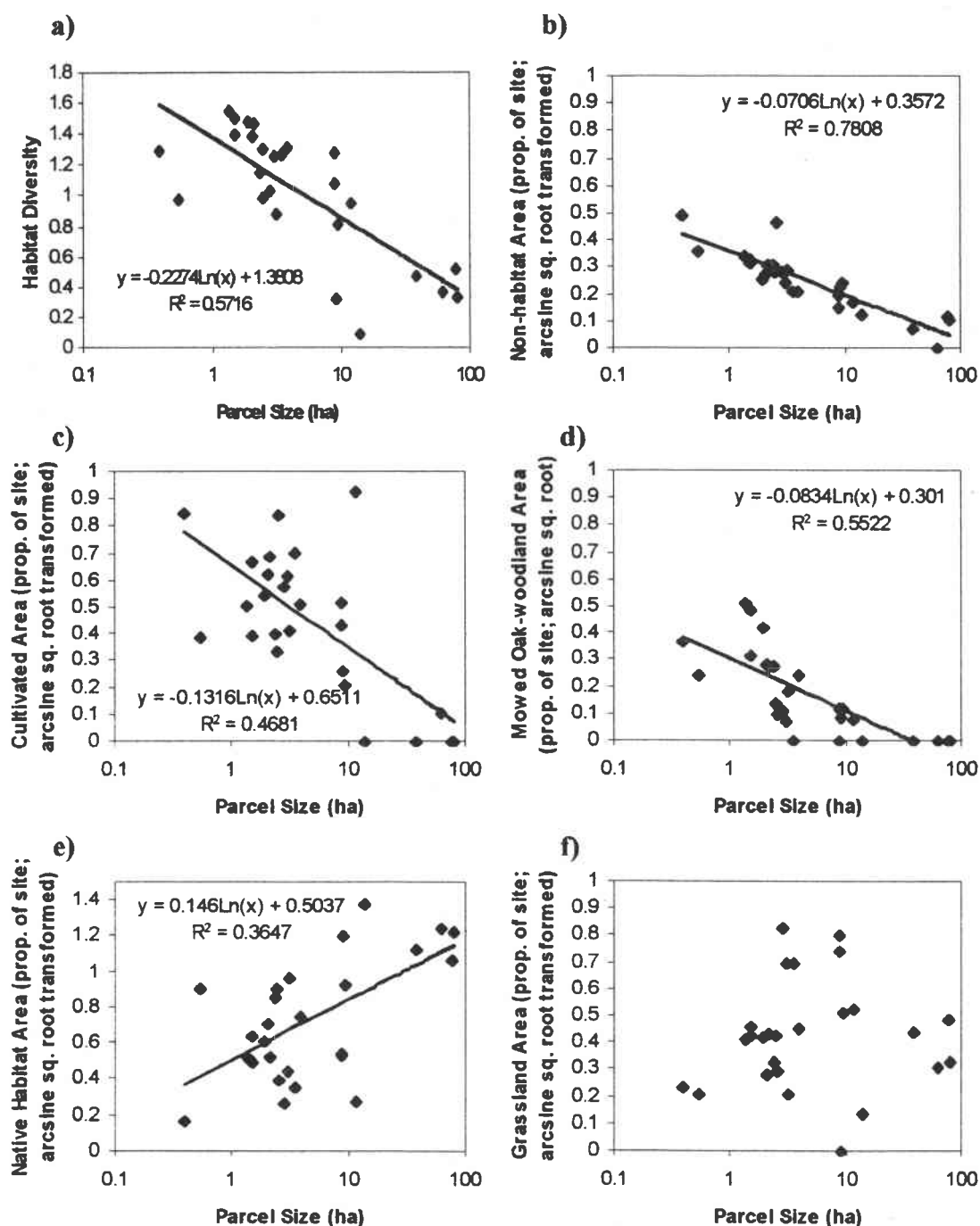
Figure 1. Site Characteristics. Relationship with the weighted average of parcel size (ha) of a) habitat diversity (p<0.001) and proportion of site area in b) non-habitat (p<0.001), c) cultivated land (p<0.001), d) mowed oak-woodland (p<0.001), e) native habitat (p=0.001), and f) grassland (p=0.749). Proportion of site area in each habitat type has been arcsine square root transformed. On Y-axis (b-f), 0.0 = 0.0 %; 0.5 = 23.0 %; 1.0 = 70.8%; and 1.5 = 99.5 % of site in given habitat type.
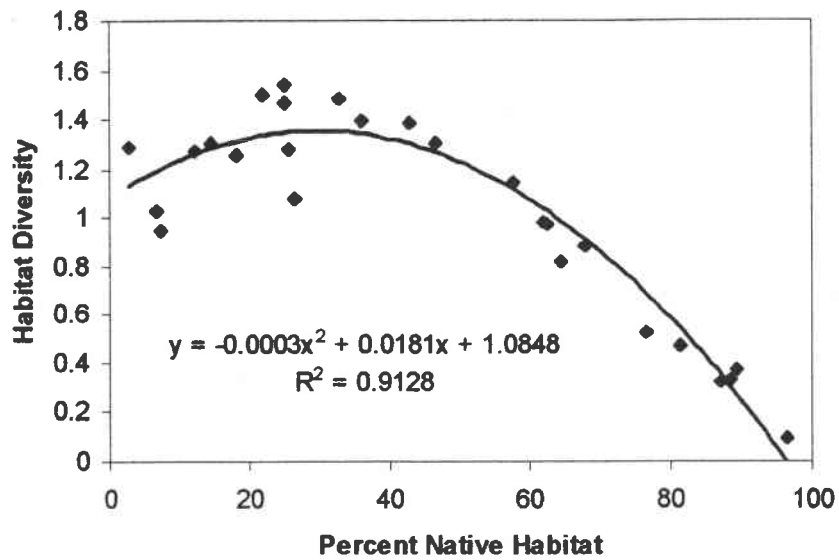
Figure 2. Relationship between habitat diversity and percent native habitat, modeled as a quadratic function (p <0.001 for each coefficient and overall regression).

a)

b)

c)
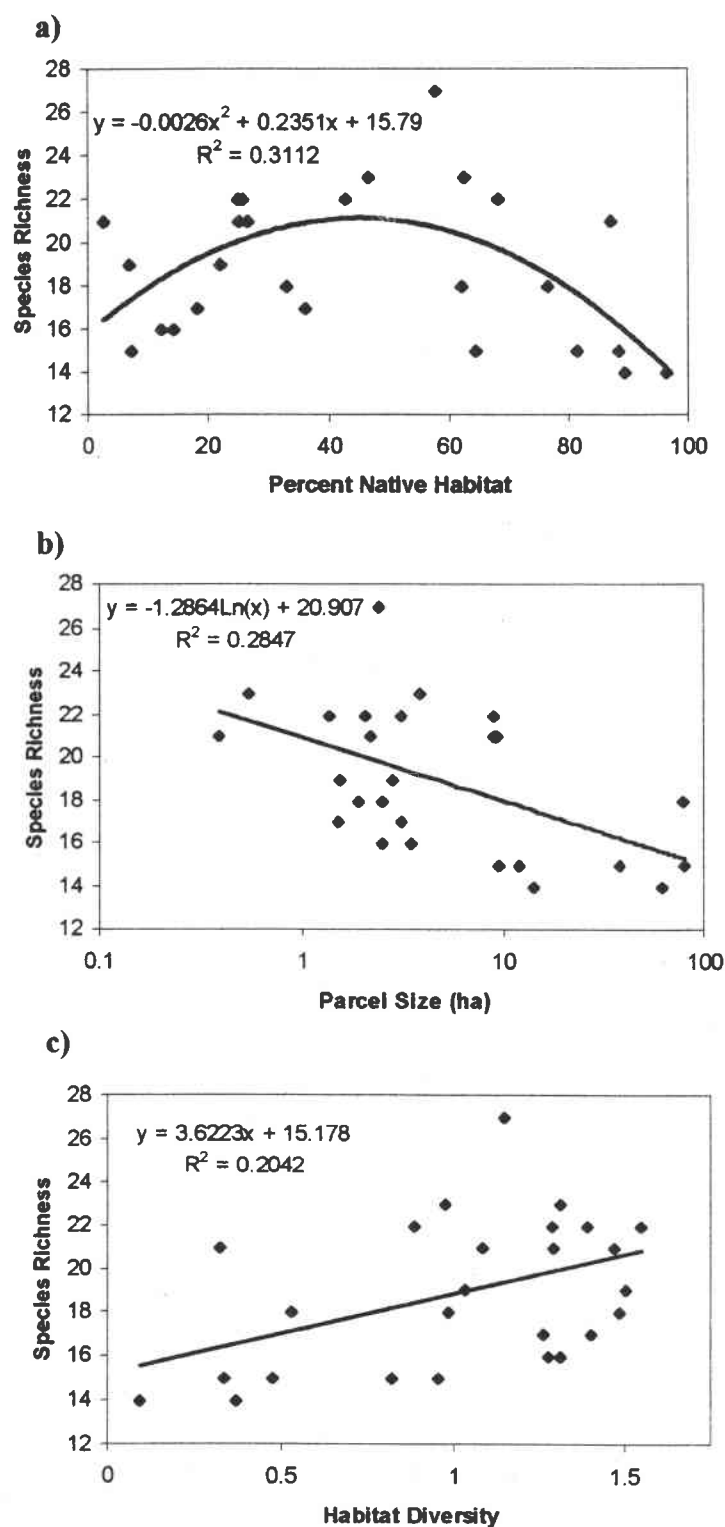
Figure 3. Relationship between species richness and a) percent area of native habitat, b) parcel size (plotted log-scale), and c) habitat diversity.
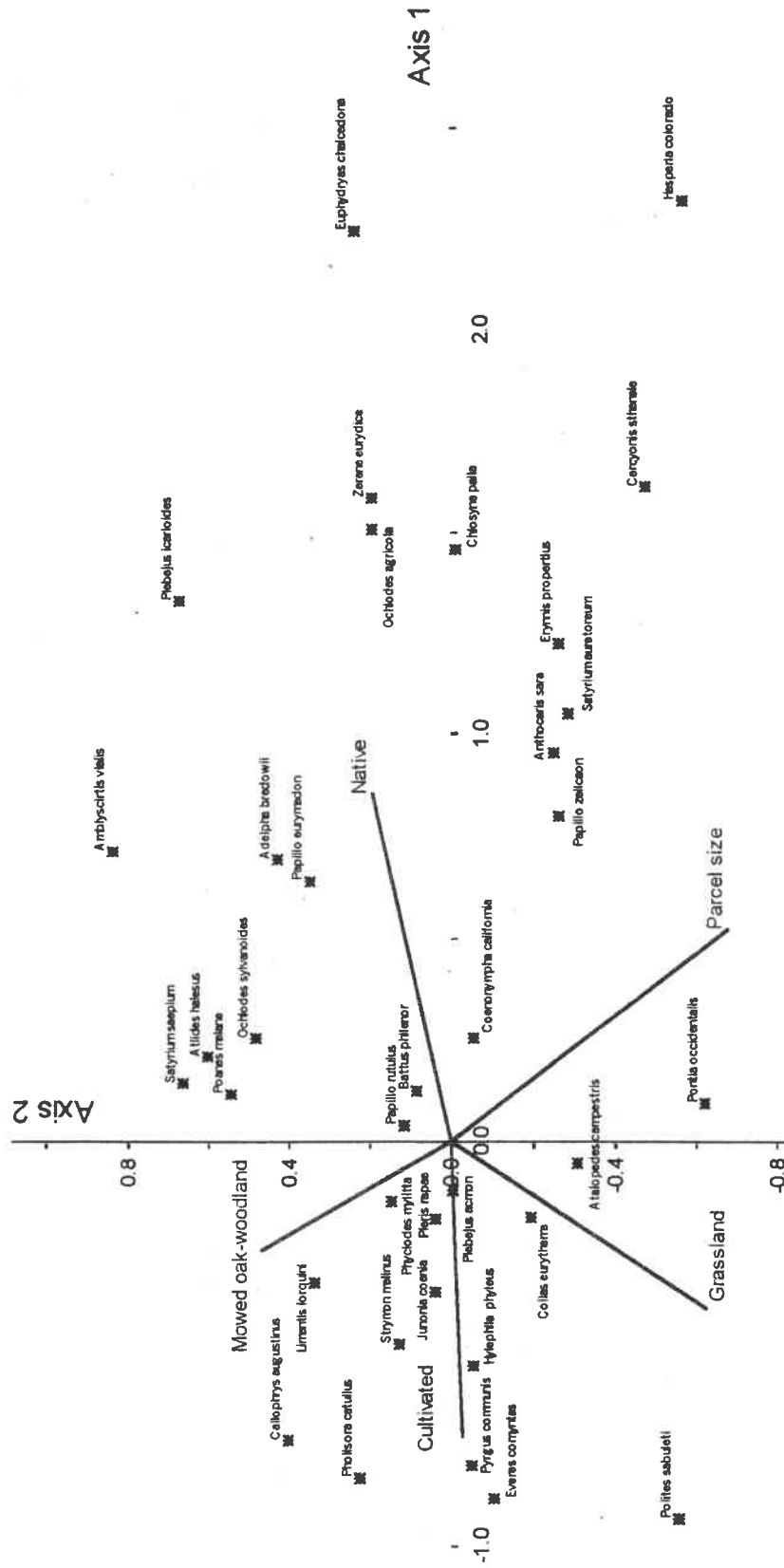
Figure 4. Ordination diagram of the canonical correspondence analysis. Although both axes are drawn, only axis 1 is significant in determining species distributions (p = 0.002). Axes are linear combinations of environmental variables (site characteristics) that maximally separate species. Environmental variable lines extend in the direction of their steepest increase. The length of a line represents the variable's importance in the model, and the angle between lines represents the correlation between variables. The distance along axis 1 at which the endpoint of an environmental variable line is perpendicular to the axis represents the correlation of that characteristic with axis 1. Likewise, the distance from the origin along an axis or an environmental variable line at which a species point is perpendicular, represents the importance of that variable or axis in determining the species' distribution. Thus, species near the origin are either uncorrelated with the environmental variables or are maximally abundant at mean levels of the variables.
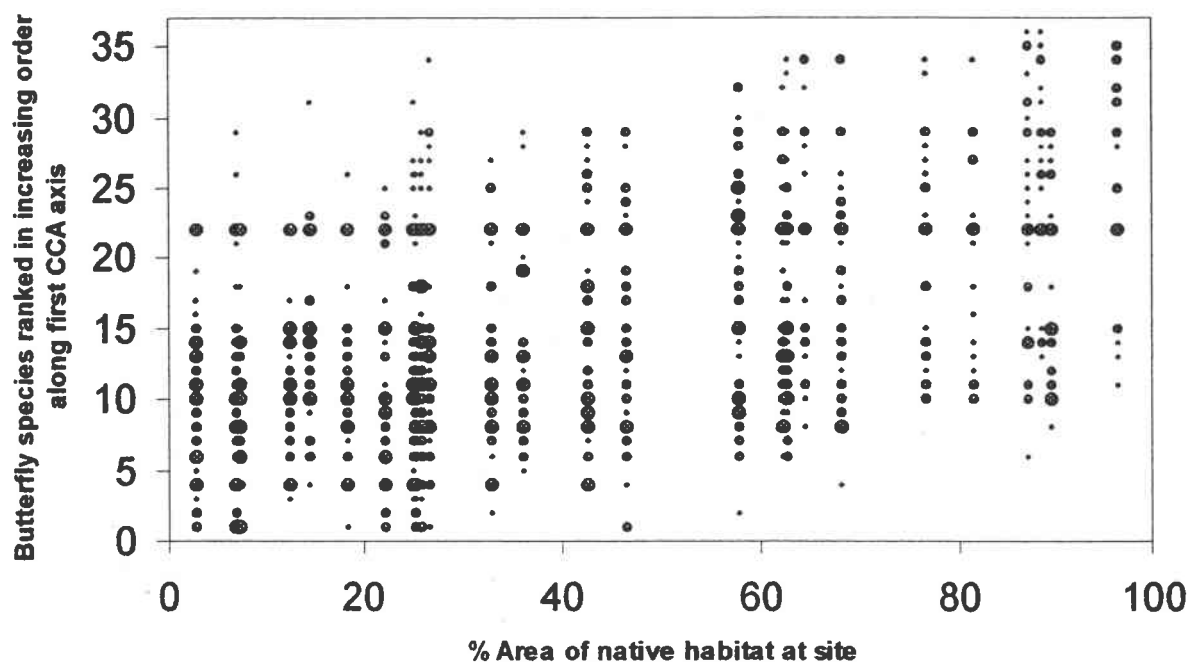
Figure 5. Frequency of species occurrences and percent area of native habitat. Points represent the occurrences of species at sites. Sites are represented by the percent area of native habitat at the site. Butterfly species are ranked by increasing species scores from the first ordination axis of the Canonical Correspondence Analysis. The size of points represents the number of occurrences of each species at sites, which range from one to nine occurrences. Greater than seven occurrences are represented by equal sized points. See Table 8 for species list.

a)

b)
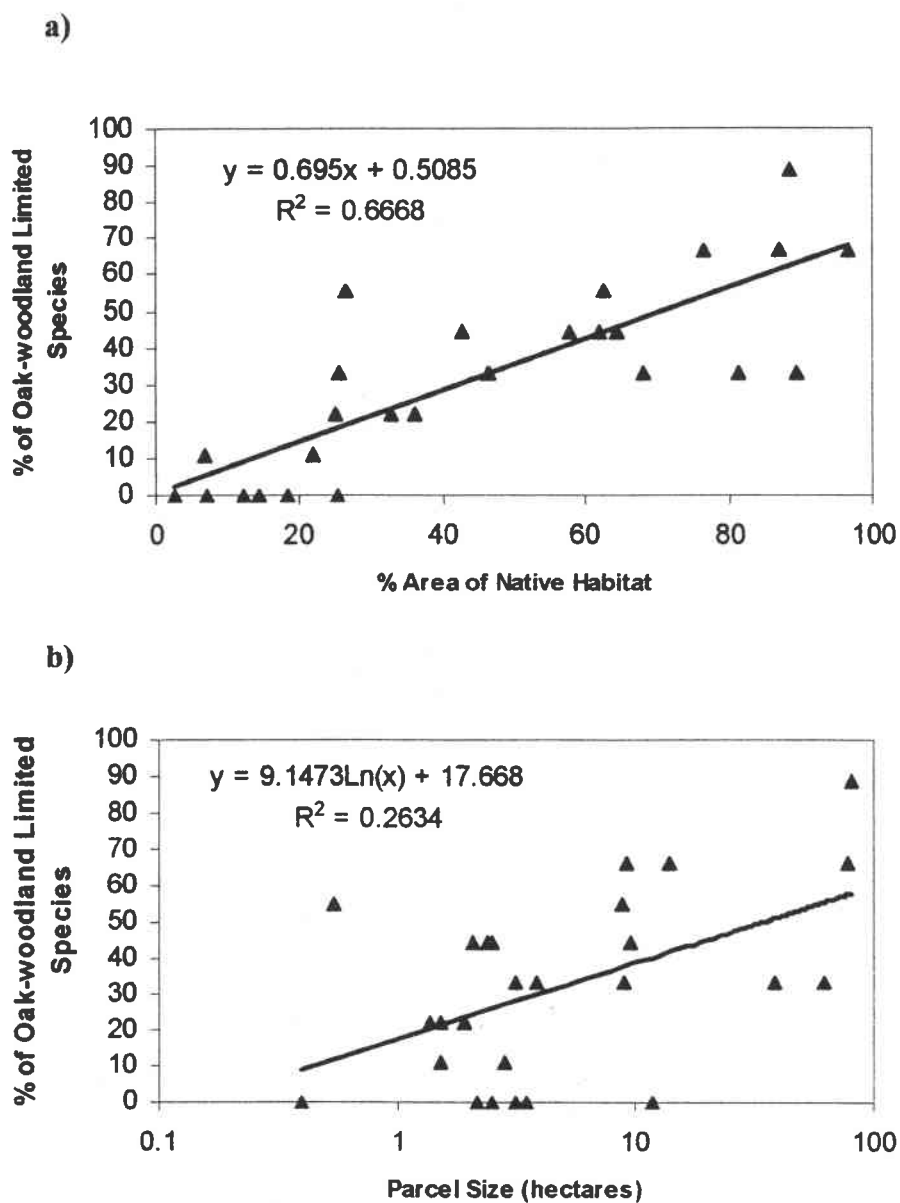
Figure 6. Response of native-habitat limited species to a) percent area of native habitat (p<0.001) and b) the natural log of parcel size (log-scale) (p=0.007). The y-axis represents the percent of nine identified native-habitat limited species occurring at a site.
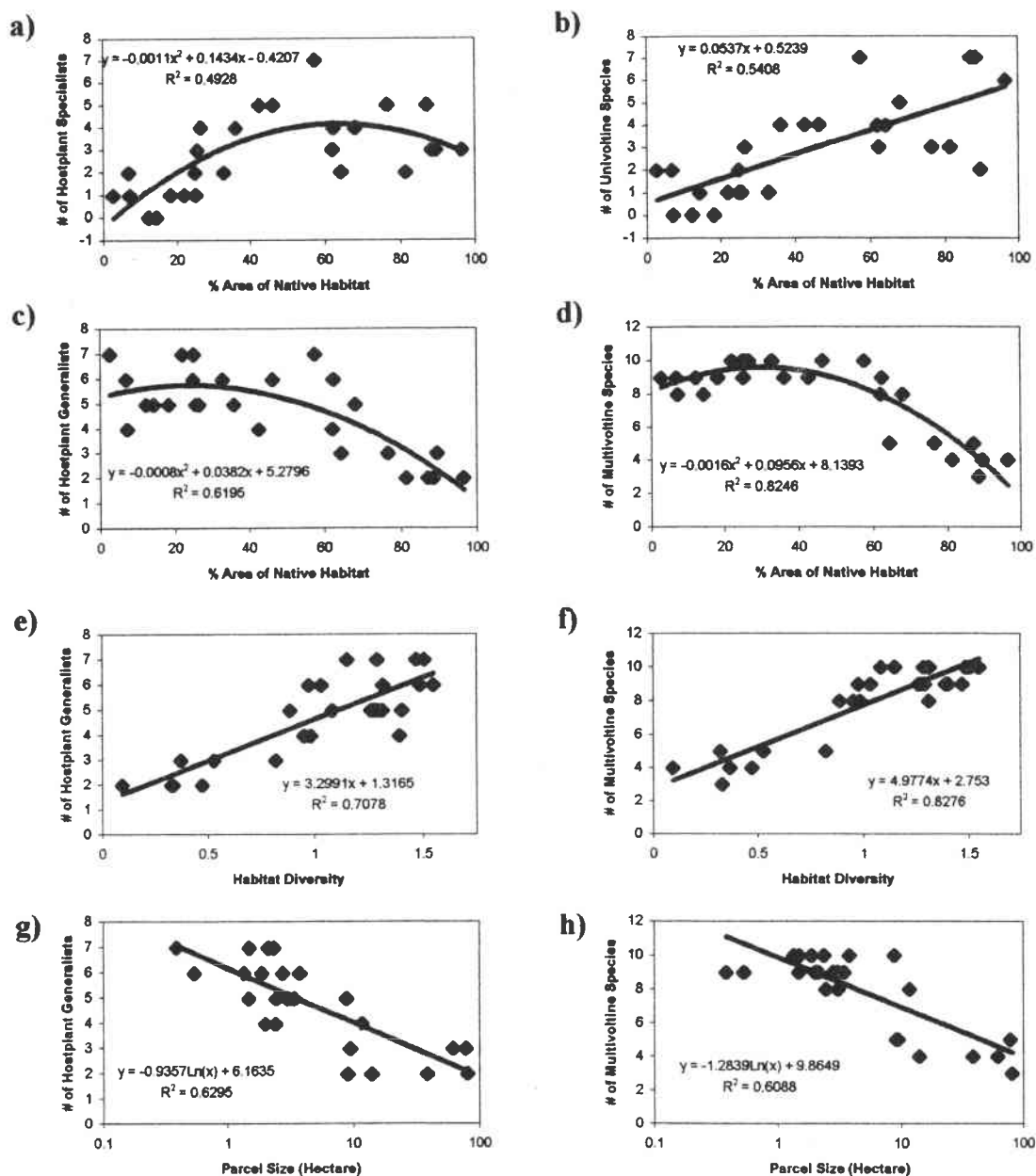
Figure 7. Relationships between richness of a) hostplant specialists, b) univoltine species, c) hostplant generalists, and d) multivoltine species and the percent area of native habitat. Relationships between richness of hostplant generalists and e) habitat diversity and g) parcel size (log-scale) and between richness of multivoltine species and f) habitat diversity and h) parcel size (log-scale). All relationships are significant (F-tests; p<0.001).
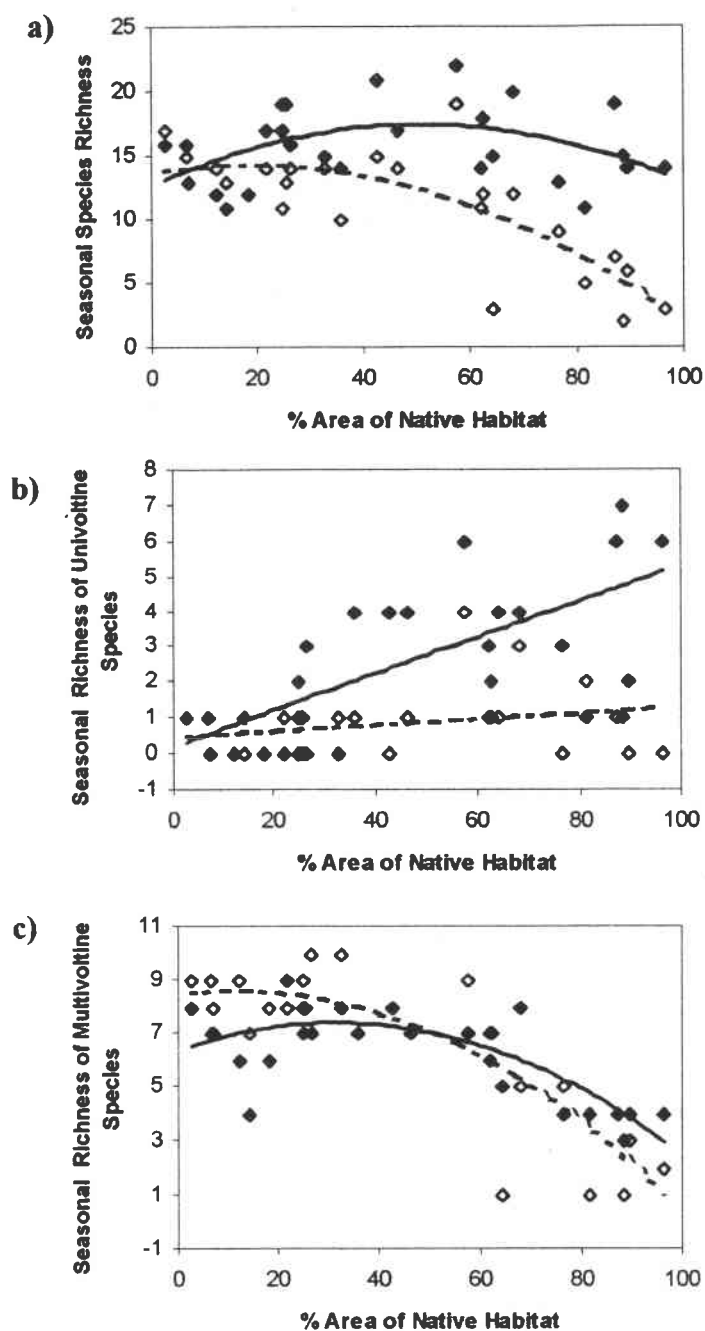
Figure 8. Seasonal responses of a) species richness, b) richness of univoltine species, and c) richness of multivoltine species to percent area of native habitat at sites. Solid diamonds represent spring richness, and the solid line is the fitted regression in spring. Open diamonds represent summer richness, and the dashed line is the fitted regression in summer.

Table 1. Relationships between habitat characteristics and the natural log of parcel size (ha). Habitat characteristics include habitat diversity and proportion of site area in non-habitat, cultivated area, mowed oak-woodland, native habitat, and grassland. All proportions were arcsine square root transformed. Standard errors in parentheses.

PREDICTOR VARIABLES	RESPONSE VARIABLE					
	Habitat Diversity	Non-Habitat	Cultivated	Mowed Oak-woodland	Native	Grassland
Constant	1.38077***	0.35717***	0.65114***	0.30098***	0.5037***	0.41301***
	(0.08424)	(0.01602)	(0.06005)	(0.03215)	(0.08248)	(0.06146)
Parcel Size	-0.22738***	-0.070643***	-0.13165***	-0.08341***	0.14602***	0.00947
	(0.04018)	(0.007641)	(0.02864)	(0.01533)	(0.03934)	(0.02932)
R-squared	57.2%	78.1%	46.8%	55.2%	36.5%	0.4%

* p < 0.05
** p < 0.01
*** p < 0.001

Table 2. Regression coefficients (standard errors) for five models of species richness with respect to percent native habitat area, the natural log of parcel size (hectares), and habitat diversity.

PREDICTOR VARIABLES	Species Richness				
	Model I	Model II	Model III	Model IV	Model V
Constant	15.790*** (1.705)	20.9073*** (0.8726)	15.178*** (1.613)	11.471* (5.409)	18.292 (1.934)
Native	0.23511* (0.08626)	----	----	0.1629 (0.1220)	0.19661 (0.08151)
Native-squared	-0.0026094** (0.0008557)	----	----	-0.001397 (0.001678)	-0.0018757 (0.0008560)
Habitat Diversity	----	----	3.622* (1.460)	3.981 (4.729)	----
Parcel Size	----	-1.2864** (0.4162)	----	----	-1.1648 (0.5226)
R-squared	31.1%	28.5%	20.4%	33.3%	43.8%

* $p < 0.05$
** $p < 0.01$
*** $p < 0.001$

Table 3. Species responses to loss of native habitat Logistic regression coefficients (standard errors) for species occurrences with respect to percent area of native habitat at sites; log likelihood for each model; p-value of G statistic based on log-likelihood values; categorization of species response (OAK - significant positive relationship with native habitat; SA - significant negative relationship with native habitat; ns - no significant response; p < 0.05).

Species	PREDICTOR VARIABLES		Log-likelihood	P-value (G-stat)	Response
	Constant	Native Habitat			
Adelpha bredowii	-0.9537 (0.7817)	0.02928 (0.01606)	-15.769	3.887*	OAK
Amblyscirtes vialis	-2.592* (1.151)	0.02261 (0.01817)	-11.894	1.670	ns
Anthocaris sara	-1.6118 (0.8478)	0.03174* (0.01584)	-15.593	4.704*	OAK
Atalopedes campestris [@]	----	----	----	----	ns
Atlides halesus	-2.575 (1.391)	0.00196 (0.02522)	-7.048	0.006	ns
Battus philenor	0.5542 (0.7607)	0.00181 (0.01423)	-16.763	0.899	ns
Callophrys augustinus	-0.510 (1.043)	-0.04672 (0.03515)	-7.892	2.812	ns
Cercyonis sthenele	-3.695** (1.376)	0.05455* (0.02162)	-11.248	9.600**	OAK
Chlosyne palla	-2.777* (1.201)	0.02584 (0.01862)	-11.662	2.132	ns
Coenonympha california [@]	----	----	----	----	ns
Colias eurytheme	11.87 (10.79)	-0.1156 (0.1226)	-2.754	2.969	ns
Erynnis propertius	-7.125 (3.747)	0.2450 (0.1349)	-4.645	25.357***	OAK
Euphydryas chalcedona	-31.63 (26.78)	0.3639 (0.3062)	-2.552	13.493***	OAK
Everes comyntas	0.727 (1.011)	-0.06955 (0.03786)	-9.218	7.020**	SA
Hesperia colorado [comma]	-11.369 (7.875)	0.12085 (0.09128)	-4.033	6.036*	OAK
Hylephila phyleus	8.420* (3.756)	-0.12157* (0.05393)	-5.930	18.430***	SA
Junonia coenia	4.436** (1.725)	-0.05694* (0.02478)	-9.834	8.422**	SA
Limentis lorquini	4.601** (1.710)	-0.06966** (0.02639)	-9.601	12.895***	SA
Ochlodes agricola	-4.405* (1.778)	0.05163* (0.02493)	-9.501	6.454*	OAK
Ochlodes sylvanoides	-0.9401 (0.7775)	0.01015 (0.01403)	-17.058	0.530	ns
Papilio eurymedon	-1.5400 (0.8394)	0.02631 (0.01516)	-16.035	3.355	ns
Papilio rutulus	3.369* (1.668)	-0.01716 (0.02593)	-6.823	0.456	ns
Papilio zelicaon	-0.7328 (0.7531)	0.01619 (0.01414)	-17.336	1.373	ns
Pholisora catullus	0.3382 (0.8534)	-0.04228 (0.02368)	-11.747	4.597*	SA
Phyciodes mylitta	13.483 (9.833)	-0.1453 (0.1126)	-3.718	6.666**	SA

Table 3. Continued...

| Species | PREDICTOR VARIABLES | | Log-likelihood | P-value (G-stat) | Response |
	Constant	Native Habitat			
Pieris rapae	51.62 (59.75)	-0.5755 (0.6733)	-1.965	10.171***	SA
Plebejus acmon	4.566* (2.068)	-0.04317 (0.02808)	-7.669	3.259	ns
Plebejus icaroides	-4.790* (2.399)	0.03922 (0.03229)	-6.075	1.952	ns
Poanes melane	0.0577 (0.7333)	-0.00821 (0.01390)	-17.536	0.354	ns
Polites sabuleti	2.226* (1.095)	-0.08059* (0.03340)	-10.118	13.305***	SA
Pontia occidentalis	-1.521 (1.054)	-0.01244 (0.02269)	-9.139	0.319	ns
Pyrgus communis	5.919** (2.263)	-0.11546** (0.04258)	-6.382	22.662***	SA
Satyrium auretoreum	-2.2728* (0.9700)	0.03728* (0.01689)	-14.334	5.978*	OAK
Satyrium saepium	-0.9816 (0.8189)	-0.00037 (0.01524)	-15.144	0.001	ns
Strymon melinus	64.85 (80.47)	-1.043 (1.286)	-1.730	30.082***	SA
Zerene eurydice	-4.981* (2.291)	0.04902 (0.03043)	-7.353	3.890*	OAK

* $p < 0.05$
** $p < 0.01$
*** $p < 0.001$
@ species occurred at all sites.

Table 4. Regression coefficients (standard errors) for response of native habitat-limited butterflies to site characteristics. Relationship between percent of identified native habitat-limited species present at a site and the percent area of native habitat, the natural log of parcel size (hectares), and percent area of grassland and of mowed oak-woodland.

PREDICTOR VARIABLE	% of Identified Native Habitat-Limited Species			
	Model I	Model II	Model III	Model IV
Constant	0.508	17.668*	0.713	-9.449
	(5.404)	(6.546)	(6.757)	(9.000)
Native	0.695***	----	0.6932***	0.7805***
	(0.1003)		(0.1081)	(0.1166)
Parcel Size	----	9.147**	----	----
		(3.122)		
Grassland	----	----	----	0.3093
				(0.2258)
Mowed Oak-woodland	----	----	-0.0244	----
			(0.4634)	
R-squared	66.7%	26.3%	66.7%	69.2%

* $p < 0.05$
** $p < 0.01$
*** $p < 0.001$

Table 5. Logistic regression coefficients for probability of occurrence for each species at each site with respect to species' life history characteristics and percent area of native habitat at sites. Interaction terms were calculated as the product of each centered variable. n = 936; 26 sites; 36 species.

Variables	Coefficients (standard errors)
constant	-3.6499***
	(0.4418)
native	-0.003796
	(0.002633)
vagility	-0.0074
	(0.1097)
hostplant breadth	0.43224***
	(0.09415)
voltinism	1.2849***
	(0.1305)
native X vagility	0.003227
	(0.003724)
native X hostplant breadth	-0.015222***
	(0.003206)
native X voltinism	-0.028658***
	(0.004278)
log-likelihood	-513.741

*** $p < 0.001$

Table 6. Regression coefficients (standard errors) for richnesses of hostplant specialists, univoltine species, hostplant generalists, and multivoltine species with respect to site characteristics. Site characteristics include percent area of native habitat at site, habitat diversity, and the natural log of parcel size (hectares).

PREDICTOR VARIABLES	RESPONSE VARIABLE (Richness of…)									
	Hostplant Specialists	Univoltine Species		Hostplant Generalists				Multivoltine Species		
Constant	1.9072*** (0.5155)	0.6721 (0.5949)	0.5239 (0.5444)	6.927*** (0.4215)	1.317* (0.4781)	7.411*** (0.3814)	7.3064*** (0.3872)	11.427*** (0.3992)	2.753*** (0.5125)	11.861*** (0.3703)
Native	0.04084*** (0.00929)	0.05583*** (0.01072)	0.05371*** (0.0101)	-0.0344*** (0.00759)	---	-0.0207* (0.0076)	-0.02091* (0.00782)	-0.4920*** (0.00719)	---	-0.0369*** (0.0074)
Native-squared	-0.00113** (0.00038)	-0.00029 (0.00044)	---	-0.00080* (0.00031)	---	-0.00040 (0.00028)	---	-0.00160*** (0.00029)	---	-0.00127*** (0.00027)
Habitat Diversity	---	---	---	---	3.299*** (0.4326)	---	---	---	4.977*** (0.4638)	---
Parcel Size	---	---	---	---	---	-0.569** (0.1719)	-1.5479*** (0.3768)	---	---	-0.5103** (0.1669)
R-squared	49.3%	54.9%	54.1%	61.9%	70.8%	74.6%	71.7%	82.5%	82.8%	87.7%

* p < 0.05
** p < 0.01
*** p < 0.001

Table 7. Linear regression coefficients (standard errors) for response of seasonal species richness and richnesses of univoltine and multivoltine species to percent area of native habitat and season (spring = 0; summer = 1).

PREDICTOR VARIABLES	RESPONSE VARIABLE		
	Species Richness	Univoltine Richness	Multivoltine Richness
Constant	16.458 ***	0.1573	8.4803 ***
	(1.079)	(0.4773)	(0.5161)
Summer	- 4.423 ***	- 1.692 ***	0.2308
	(0.7904)	(0.3638)	(0.378)
Native	0.0195	0.0516 ***	- 0.0292 **
	(0.0197)	(0.00886)	(0.00943)
Native X Summer	- 0.119 ***	- 0.0433 ***	- 0.0408 **
	(0.0272)	(0.01253)	(0.01302)
Native-squared	- 0.00187 **	-----	- 0.00105 ***
	(0.000585)		(0.000280)
R-squared	61.80%	54.10%	68.40%

** p < 0.01
*** p < 0.001

Table 8. Non-migrant species that occurred at more than one site and their responses to loss of native habitat. Species rank is their order along the first CCA ordination axis (see text). Number of occurrences is the total number of visits to sites during which the species was observed (out of 234 vists to 26 sites). Species responses are the classification of species with respect to native habitat decline in each of four studies.

Species	Species Rank	# of occur.	This study	Blair and Launer (1997)[a]	Merendlender et al. (1998)[b]	Shapiro (1980, 1987)[c]
Polites sabuleti	1	28	SA	SA[g]	--	SA[1]
Everes comyntas	2	5	SA	--	--	SA[1]
Pholisora catullus	3	13	SA	--	--	SA[1,2]
Pyrgus communis	4	71	SA	SA[g]	ns	SA[1,2]
Callophrys augustinus	5	3	ns	--	--	--
Hylephila phyleus	6	63	SA	SA[r]	--	SA[1,2]
Strymon melinus	7	38	SA	SA[r]	--	SA[1,2]
Junonia coenia	8	85	SA	SA[os]	ns	SA[1,2]
Limentis lorquini	9	43	SA	--	--	--
Pieris rapae	10	116	SA	SA[r]	ns	SA[1,2]
Colias eurytheme	11	103	ns	SA[os]	ns	SA[1]
Phyciodes mylitta	12	86	SA	SA[os]	ns	SA[1,2]
Plebejus acmon	13	72	ns	SA[os]	--	SA[1]
Atalopedes campestris	14	95	ns	SA[r]	--	SA[1]
Papilio rutulus	15	92	ns	SA[r]	ns	SA[1]
Pontia occidentalis	16	3	ns	--	--	--
Poanes melane	17	19	ns	ns	--	OAK[2]
Battus philenor	18	39	ns	--	ns	OAK[2]
Satyrium saepium	19	16	ns	--	--	--
Atlides halesus	20	2	ns	--	--	SA[1]
Coenonympha california	21	200	ns	OAK	ns	OAK[1]
Ochlodes sylvanoides	22	11	ns	OAK	--	OAK[2]
Papilio eurymedon	23	20	ns	--	ns	OAK[2]
Adelpha bredowii	24	29	ns	--	ns	OAK[1,2]
Amblyscirtes vialis	25	8	ns	--	--	--
Papilio zelicaon	26	18	ns	--	ns	SA[1,2]
Anthocaris sara	27	14	OAK	SA[os]	--	--
Satyrium auretoreum	28	11	OAK	--	--	OAK[2]
Erynnis propertius	29	42	OAK	OAK	ns	--
Plebejus icaroides	30	2	ns	--	--	--
Chlosyne palla	31	7	ns	--	ns	--
Ochlodes agricola	32	7	OAK	OAK	ns	--
Zerene eurydice	33	3	OAK	--	--	OAK[1]
Cercyonis sthenele	34	15	OAK	--	--	--
Euphydryas chalcedona	35	6	OAK	OAK	ns	OAK[1,2]
Hesperia colorado [comma]	36	2	OAK	OAK	--	--

[a] Palo Alto, coastal central California (CA), USA, [b] Sonoma County, northwestern CA, USA, [c] Davis, central valley, CA
OAK, native habitat limited; [1] uncommon or non-breeding in highly modified central valley, CA (Shapiro 1980);
[2] previously occurred in the central valley, CA, but has declined or disappeared (Shapiro 1987).
SA, suburban adaptable (more common at less native sites); [os] peak abundance at open-space preserve; [g] peak abundance at golf course; [r] peak abundance in residential area; [1] identified as "weedy" species or as breeding on cultivated plants (Shapiro 1980); [2] widespread species that feed almost exclusively on weedy hosts (Shapiro 1987).
ns, no significant response to native habitat area; --, not sampled.

Appendix 1. Non-migratory species that occurred at more than one site and life history data used in analyses.

Species	Common Name	Vagility[a]	Hostplant Breadth[b]	Voltinism[c]	Hostplants[d]	Habitat[e]
Hesperiidae						
Amblyscirtes vialis	Roadside skipper	2	3	1	grasses	west slope of Sierra
Atalopedes campestris	Field skipper, Sachem	4	3	2	grasses	fields, cut-over land, meadowes, vacant lots, roadsides
Erynnis propertius	Propertius dusky-wing	3	2	1	oaks, including *Quercus agrifolia* and *Q. garryana*	Open oak woodlands, forest openings and edges, meadows and fields near oaks
Hesperia colorado (comma)	Western banded skipper	3	3	1	grasses	Sunny open areas including forest openings and edges, meadows, fields, roadsides, trails, grassy slopes, and the alpine. cultivated areas such as lawns, yards, fence rows, edges of swamps and marshes, abandoned fields, and vacant lots; rare in undisturbed backlands
Hylephila phyleus	Fiery skipper	4	3	3	grasses	streamsides, forest edges, roadsides, meadows
Ochlodes agricola	The farmer, Rural Skipper	2	3	1	grasses	Grassy areas in chaparral, sagebrush, woodland, gardens, and small streams.
Ochlodes sylvanoides	Woodland skipper	2	3	1	various grasses	widely distributed but uncommon
Pholisora catullus	Common sooty-wing	2	4	1.5	*Chenopodium* spp. and *Amaranthus* spp.	streamsides, clearings, trails, roadsides
Poanes melane	Umber skipper	3	3	2	grasses	Alkali grasslands, moist meadows, lawns, salt marshes, sand dunes, sagebrush flats, and alpine fell-fields.
Polites sabuleti	Sandhill skipper	2	3	2	*Distichlis spicata*, Bermuda grass, and others	backyards, vacant lots, city parks, fields, cultivated lands, roadsides
Pyrgus communis	Common checkered skipper	4	3	3	members of Mallow family	oak woodlands, along stream bottoms
Lycaenidae						
Atlides halesus	Great purple hairstreak	3	1	3	*Phoradendron flavescens*	
Callophrys [Incisalia] augustinus	Western brown elfin	1	4	1	mostly buds and flowers of *Cuscuta* spp., *Ceanothus* spp., *Arbutus menziesii*, and *Chlorogalum pomeridianum*	chapparal and forest edges
Everes comyntas	Eastern tailed blue	2	3	1.5	various herbaceous legumes	moist places, marshy land
Plebejus acmon	Acmon blue	2	4	3	various legumes plus *Eriogonum*	very general
Plebejus icarioides	Icarioides blue	2	2	1	various perennial lupines	general montane
Satyrium auretorum	Gold-hunter's hairstreak	2	2	1	Oaks, especially *Q. douglasii*, *Q. dumosa*, and *Q. wislizenii*	foothills and moderate elevations
Satyrium saepium	Hedge-row hairstreak	2	2	1	*Ceanothus* spp.	chaparral and forest edges
Strymon melinus	Common hairstreak	4	4	3	buds and young seeds of many plants across several families	Grassy areas in chaparral, sagebrush, woodland, gardens, and small streams.
Nymphalidae						
Adelpha bredowii	California sister	4	2	2.5	various oaks, especially *Q. chrysolepis*, *Q. agrifolia*, and *Q. vaccinifolia*	Oak-covered hills, groves, and stream valleys.
Chlosyne palla	Northern checkerspot	3	3	1	Asteraceae	Coastal chaparral, open woodland, sagebrush, meadows,
Euphydryas chalcedona	Common checkerspot	3	3	1	Figwort family	coniferous woodlands both ES and WS, sagebrush ES
Junonia coenia	Buckeye	4	4	2.5	Plantaginacee, *Antirrhinum majus*, and *Mimulus* spp.	weedy pastures, roadsides, yards
Limenitis [Basilarchia] lorquini	Lorquin's admiral	2	4	2.5	*Salix* spp., *Populus* spp., *Prunus* spp.	streams and moist meadows
Phyciodes mylitta	Mylitta crescent	2	3	2	thistles (*Cirsium* spp.) and *Silybum marianum*	From sea level to 8000 feet in mountains, fields, meadows, roads, vacant lots, parks, and fencerows.

Species	Common Name	Vagility[a]	Hostplant Breadth[b]	Voltinism[c]	Hostplants[d]	Habitat[d]
Papilionidae						
Battus philenor	Pipevine swallowtail	3	1	2	Dutchman's Pipe (*Aristolochia californica*)	A wide variety of open habitats, open woodland, and woodland edges.
Papilio eurymedon	Pale swallowtail	3	4	2	*Rhamnus* spp., *Ceanothus* spp., and *Prunus ilicifolia*	hills, mountains, canyons
Papilio rutulus	Western tiger swallowtail	3	4	2	many deciduous broad-leaved trees	parks, backyards, riparian areas
Papilio zelicaon	Anise swallowtail	3	3	2	originally members of Parsley family, now mostly *Foeniculum vulgare* and *Daucus carota*	vacant lots, hills, and fields
Pieridae						
Anthocharis sara	Sara orange-tip	2	3	2	many members of the Mustard family	Open oak woods in hills, orchards, fields, meadows, streamcourses, canyons.
Colias eurytheme	Common sulfur	4	3	4	members of Pea family	pest of alfalfa
Pieris rapae	Cabbage butterfly	4	3	4	most members of Mustard family	Almost any type of open space including weedy areas, gardens, roadsides, cities, and suburbs.
Pontia occidentalis	Western white	4	3	2	various mustards-Mustard family	Mountain peaks, slopes, hilltops, railroad yards, open plains, roadsides.
Zerene eurydice	California dog-face	3	1	2	False indigo (*Amorpha californica*)	Foothills, chaparral, oak or coniferous woodlands
Satyridae						
Cercyonis sthenele	Little satyr	2	3	1	grasses-Poaceae	open woodlands
Coenonympha tullia california	California ringlet	2	3	3	grasses - Poaceae	almost everywhere

[a] 1, disperse 10's of meters; 2, disperse 100's of meters; 3, disperse 1000's of meters; 4, disperse 10,000's of meters or more (George Austin, personal communication)

[b] 1, feed on single plant species; 2, feed on plants from single genus; 3, feed on plants from multiple families (Garth and Tilden, 1986)

[c] typical number of broods for the species (Garth and Tilden, 1986). Average number of broods used if range was provided; "multiple" and "many" broods were scored as three broods.

[d] (Garth and Tilden, 1986)